



Variation for root aerenchyma formation in flooded and non-flooded maize and teosinte seedlings

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Abstract

Morphological and anatomical factors such as aerenchyma formation in roots and the development of adventitious roots are considered to be amongst the most important developmental characteristics affecting flooding tolerance. In this study we investigated the lengths of adventitious roots and their capacity to form aerenchyma in three- and four-week-old seedlings of two maize (*Zea mays* ssp. *mays*, Linn.) inbred accessions, B64 and Na4, and one teosinte, *Z. nicaraguensis* Iltis & Benz (Poaceae), with and without a flooding treatment. Three weeks after sowing and following a seven day flooding treatment, both maize and teosinte seedlings formed aerenchyma in the cortex of the adventitious roots of the first three nodes. The degree of aerenchyma formation in the three genotypes increased with a second week of flooding treatment. In drained soil, the two maize accessions failed to form aerenchyma. In *Z. nicaraguensis*, aerenchyma developed in roots located at the first two nodes three weeks after sowing. In the fourth week, aerenchyma developed in roots of the third node, with a subsequent increase in aerenchyma in the second node roots. In a second experiment, we investigated the capacity of aerenchyma to develop in drained soil. An additional three teosinte species and 15 maize inbred lines, among them a set of flooding-tolerant maize lines, were evaluated. Evaluations indicate that accessions of *Z. luxurians* (Durieu & Asch. Bird) and two maize inbreds, B55 and Mo20W, form aerenchyma when not flooded. These materials may be useful genetic resources for the development of flooding-tolerant maize accessions.

Introduction

In the Asian monsoon region, soil flooding during the late spring and early summer is a major source of environmental stress for summer crops of maize, sorghum and soybean. Low oxygen concentration in the rhizosphere results from flooding and leads to a reduction of plant

growth. Two primary factors affecting flooding tolerance in plants have been reported including their capacity to form aerenchyma channels in roots (Arikado and Adachi, 1955; Armstrong et al., 1991; Burdick, 1989; Jat et al., 1975; McDonald et al., 2001) and their ability to grow adventitious roots at the soil surface (Bird, 2000; Lizaso et al., 2001; Mano et al., 2005a). In studies of barley, an association between flooding tolerance and both aerenchyma formation and adventitious root development has been

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suggested with several genotypes exhibiting superior tolerance to flooded rice paddy field conditions being identified (Stanca et al., 2003; Takeda, 1989).

Rice and other wetland species grow well under flooded conditions, at least in part, by supplying oxygen through root aerenchyma. In various studies, two types of aerenchyma have been observed in roots: (1) lysigenous aerenchyma, caused by the selective death of some cortical cells; and (2) schizogenous aerenchyma, formed by cell separation (Evans, 2003). Lysigenous aerenchyma induced by hypoxia or low-oxygen levels during flooding and mediated by ethylene has been well documented in maize using molecular and cellular analyses (Gunawardena et al., 2001; He et al., 1996; Jackson et al., 1985; Jat et al., 1975; Saab and Sachs, 1996; Subbaiah and Sachs, 2003). Maize does not typically form aerenchyma in non-flooding or non-stressed conditions but can form lysigenous aerenchyma in aerated hydroponic cultivation of seedlings if nitrogen levels are low (Konings and Verschuren, 1980). Although aerenchyma formation in maize roots has been investigated when not flooded (Jat et al., 1975), an evaluation of the capacity of various genotypes to form aerenchyma at a relatively early growth stage, when severe damage can be caused by flooding, has not been reported. Also, little is known about varietal variation for aerenchyma formation in maize in non-flooding conditions.

The 'maize-like' wild relatives of cultivated maize (*Zea mays*) are accumulatively known as 'teosinte'. However, *Zea mays*, consists of several teosintoid type subspecies such as *Zea mays* ssp. *mexicana* (Schrad.) Iltis, *Z. mays* ssp. *parviglumis* (Iltis & Doebley) and *Z. mays* ssp. *huehuetenangensis* (Iltis & Doebley). The term 'teosinte' also refers to at least four taxonomically distinct species, *Zea diploperennis* (Iltis, Doebley & Guzman), *Z. perennis* (Hitchc.), Reeves & Mangelsdorf *Z. luxurians* (Durieu & Asch. Bird) and *Z. nicaraguensis* (Iltis & Benz). In this research, we focus specifically on aerenchyma formation and transference from *Zea luxurians* and *Z. nicaraguensis* to cultivated maize. In an earlier study, under well-aerated, non-flooded conditions, *Z. luxurians* was reported to develop well-formed aerenchyma in adult plants (Ray et al., 1999). This observation suggests that if a plant possesses aerenchyma

channels in a non-stressed or non-flooded condition, it may be able to adapt more rapidly to flooding conditions.

We previously investigated varietal variation in maize, teosinte and their hybrids for adventitious root formation at the soil surface during flooding and successfully identified QTLs for the trait (Mano et al., 2005a,b,c). We are working to transfer these QTLs from teosinte to maize by a marker-assisted backcrossing approach (Y. Mano unpublished). Additional selection for flooding tolerance via aerenchyma channel generation should help in developing superior and stable flooding-tolerant maize lines.

Our objectives for this study were: (1) to investigate maize and teosinte seedlings in greater detail with regard to the formation of aerenchyma in several parts of adventitious roots with and without flooding; (2) to evaluate aerenchyma-forming capacity in maize and teosinte materials that exhibit varied levels of flooding tolerance at the seedling stage (Mano et al., 2002); and (3) to identify materials exhibiting a high capacity to form aerenchyma that may serve as useful genetic resources for the breeding of flooding tolerant accessions of maize.

Materials and methods

Experiment 1: Comparisons of root aerenchyma development with and without flooding

Plant materials

The yellow dent Iowa maize inbred line, B64, was provided by the Genebank, National Institute of Agrobiological Sciences, Tsukuba, Japan (00094105). The Japanese subtropical yellow flint maize inbred, Na4, was obtained from the Corn and Sorghum Breeding Laboratory, National Institute of Livestock and Grassland Science, Nasushiobara, Japan. *Z. nicaraguensis* (CI-MMYT 13451) was provided by the International Maize and Wheat Improvement Center (CI-MMYT), Mexico. Prior evaluations have shown that B64 is sensitive to flooding, whereas Na4 and *Z. nicaraguensis* (from a frequently flooded coastal plain in northwest Nicaragua) are tolerant of flooding (Bird, 2000; Iltis and Benz, 2000; Mano et al., 2002; Y. Mano unpublished).

Flooding treatment

Experiment 1 was conducted in a greenhouse maintained at a temperature of 30 °C day/25 °C night with natural light at 13–14 h day length. For the flooding treatment, the three accessions were grown in 11 cm diameter, 15 cm deep pots filled with granular soil (Kureha Chemical Industry, Tokyo Japan; 0.6 g N, 2.9 g P, 0.9 g K in each pot) with one plant per pot. The seedlings were grown to the four-leaf stage (two weeks after sowing), and were then flooded for two weeks with the water level being kept 3 cm above the soil surface. For the non-flooded control (i.e. drained soil), seedlings were grown in pots 11 cm in diameter and 30 cm deep (1.2 g N, 5.8 g P, 1.8 g K in each pot). The difference between pot depth of the flooded and drained treatments was used to help discriminate between classes of individuals that would or could not form aerenchyma. It had been previously observed that in the 15 cm pots with drained soil, aerenchyma was formed in many lines. It is believed that as the roots come in contact with each other in the more shallow pots, aerenchyma formation resulted (Y. Mano unpublished). As a consequence, 30 cm deep pots were utilized to reduce or eliminate this behavior. The seedlings were irrigated every third or fourth days with water. At three and four weeks following sowing (equaling one and two weeks of flooding in the flooding treatment), adventitious or shoot-borne crown roots of flooded plants and control plants were collected for sectioning and aerenchyma measurement.

Root anatomy

For both treatments, two plants exhibiting similar vegetative growth were evaluated. For each individual plant, a total of four to six adventitious roots at each of four nodes (first (lower) to fourth (upper)) were evaluated for the presence of aerenchyma.

Cross sections of fresh roots exhibiting a thickness of 80–100 μm were made every 5 cm starting 0.5 cm beyond the root base (root-shoot junction). A microtome (MTH-1, Nippon Medical & Chemical Instruments Co. Ltd., Osaka, Japan) was used to prepare the cross sections. Fixation or mounting in wax media was unnecessary. The amount of aerenchyma in the root cortex was visually scored: 0 (no aerenchyma),

0.5 (partial formation), 1 (radial formation), 2 (radial formation extended toward epidermis) and 3 (well-formed aerenchyma). These values corresponded to an approximate percentage of aerenchyma in the cortex of 0 %, ~10 %, ~20 %, ~35 % and over 35 %, respectively.

Experiment 2: Screening for aerenchyma-forming accessions in a non-stressed condition

Plant materials and treatment

In Experiment 2, four-week old seedlings of 17 maize inbred accessions and four teosintes, including the accessions B64, Na4 and *Z. nica-raguensis* evaluated in Experiment 1 were used (Table 1). Growing conditions were the same as those in Experiment 1. In a previous study using 223 maize inbred lines indicated that six of the maize lines tolerated flooding (B55, N196, A15, B73, Na4 and Na74), and five accessions were sensitive to flooding (A96, B64, H84, Pa91 and Mo17) at the seedling stage (Mano et al., 2002). Seedlings were grown without flooding (i.e. in drained soil).

Root anatomy

Aerenchyma was observed in adventitious roots as described in Experiment 1 with the following minor differences. Six plants per line were evaluated. Adventitious roots were collected only from the second nodes and were evaluated for the amount of aerenchyma at four weeks after sowing. Cross sections were made every 5 cm starting from the root base. Since it has been determined that younger roots in non-flooding conditions may not form aerenchyma, even in the aerenchyma-forming accessions (Y. Mano, unpublished), only older adventitious roots longer than 20 cm were evaluated.

Results

Experiment 1: Comparisons of root aerenchyma with and without flooding using two maize lines and one teosinte

Following a two-week flooding treatment, at the lower two nodes, the lengths of the roots were generally less than for the controls, below 15 cm

Table 1. Comparison of the extent of aerenchyma formation in the cortex of adventitious roots of four-week old plants in four teosintes and 17 maize inbred lines contrasting flooding tolerance grown in well-drained soil

Accession	Code	Source	FL tolerance ^a	Aerenchyma ^b	No. of plants tested	No. of roots obs ^c	No. of portions obs ^d
Teosinte							
<i>Z. nicaraguensis</i>	CIMMYT13451	CIMMYT	T	+	6	14	83
<i>Z. luxurians</i>	PI441933	USDA	No data	+	6	15	99
<i>Z. mays</i> ssp.	PI441934	USDA	T	–	6	16	77
Huehuetenangensis							
<i>Z. mays</i> ssp. <i>mexicana</i>	Ames8083	USDA	No data	–	6	12	80
Maize							
B55	–	NILGS	T	+	6	15	92
Mo20W	–	NILGS	M	+	6	11	67
N196	00076759	NIAR	T	+–	5	11	65
A15	00000810	NIAR	T	+–	6	13	74
CML-155	00090528	NIAR	M	+–	6	11	71
B73	–	NILGS	T	–	6	9	51
Na4	–	NILGS	T	–	6	10	66
Na74	–	NILGS	T	–	5	10	58
H107	00041248	NIAR	M	–	6	10	57
OH33	00003223	NIAR	M	–	5	8	42
OH43	45009759	NIAR	M	–	5	8	51
P39	00000920	NIAR	M	–	5	10	57
A96	00003113	NIAR	S	–	6	10	63
B64	00094105	NIAR	S	–	6	8	49
H84	45009662	NIAR	S	–	5	13	67
Pa91	00094116	NIAR	S	–	6	13	72
Mo17	–	NILGS	S	–	5	11	43

Sections were taken from the base of roots over 20 cm long that emerged from the second oldest coleoptilar node.

^aFlooding tolerance evaluated by the dry weight ratio of shoot (treatment/control) in the study of Mano et al. (2002) and Y. Mano (unpublished).

T; tolerant, M; moderate, S; sensitive.

^bAerenchyma-forming capacity at non-flooding condition (+:presence, +–:slightly formed, –:absence).

^cNumber of adventitious roots observed.

^dAerenchyma was observed every 5 cm portions from the root-shoot junction.

in all three accessions (Figure 1). However, root lengths at the third and fourth nodes were increased by the flooding treatment, and the total number of roots was seen to increase (data not shown). Both the primary and seminal roots became necrotic during the flooding treatment and, as such, were not considered an important component in a plant's response or adaptation to flooding, so we did not evaluate these root types in the experiment.

All three accessions formed aerenchyma in the basal portion (towards root-shoot junction) of the root and the gradient of aerenchyma from the base to tip was observed at one week of flooding treatment. With two weeks of treatment, the degree of aerenchyma formation in all three

accessions increased in the roots that had emerged from the first to fourth nodes (Figures 2–3). *Z. nicaraguensis* generally exhibited a higher or equivalent capacity for aerenchyma formation at nodes two to four and at all distances from the root base when compared to B64 or Na4. In some instances, a unique morphology was found: small lateral roots were observed to form in aerenchyma channels at the basal portion of the adventitious roots of flooded *Z. nicaraguensis* and Na4 (Figure 2d, shown in arrow).

When not flooded, the two maize accessions (B64, Na4) did not form aerenchyma, whereas the *Z. nicaraguensis* accession was observed to form aerenchyma (Figure 3). After only two

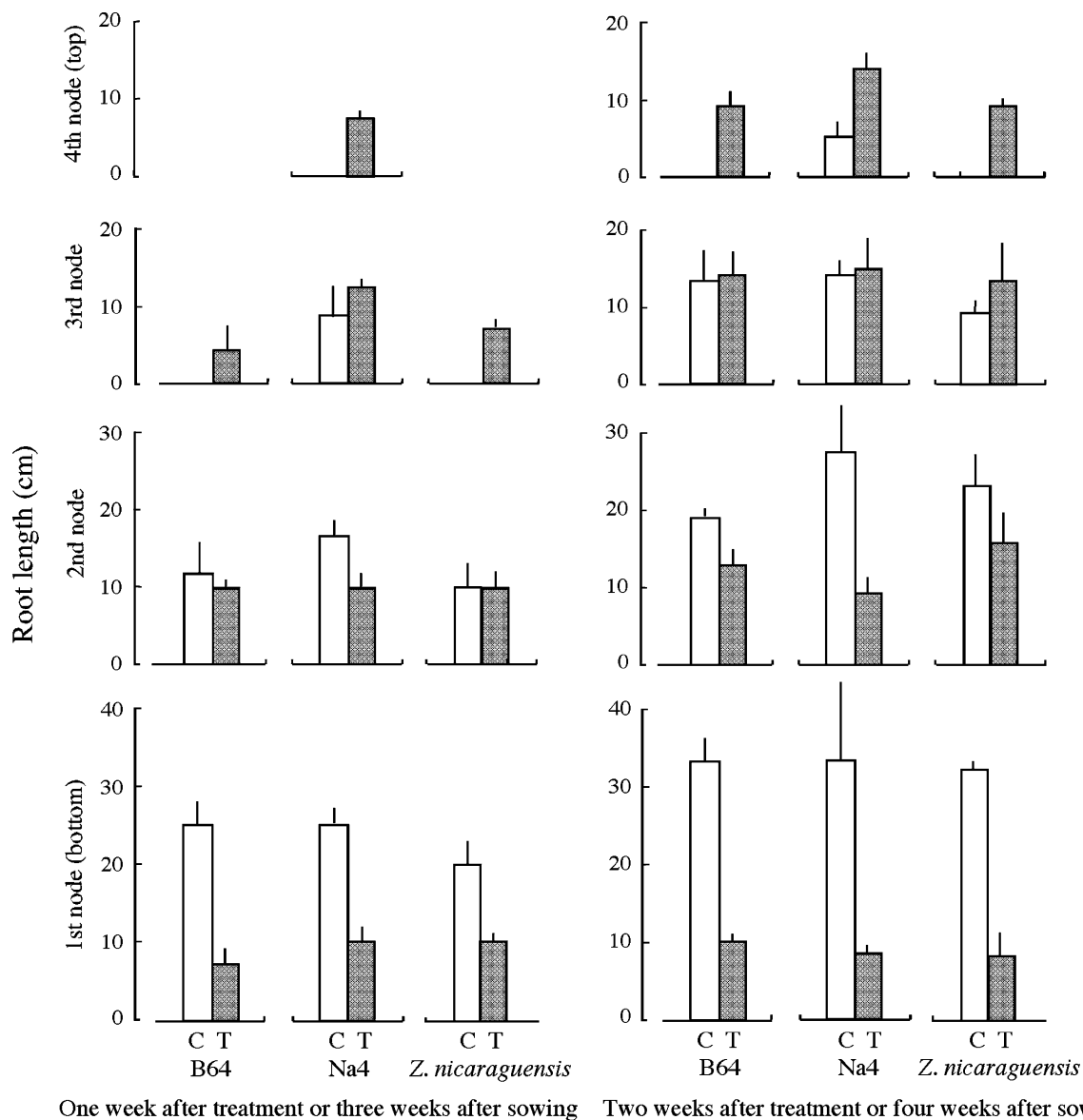


Figure 1. Comparisons of root lengths among three accessions with non-stressed control (white bars) and flooding treatment (shaded bars) with one week of treatment or three weeks after sowing (left) and with two weeks of treatment or four weeks after sowing (right). The values are the means of 4–6 roots pooled from two plants \pm standard deviations.

weeks post-sowing, evaluations of *Z. nicaraguensis* roots indicated a slight formation of aerenchyma (data not shown). In the non-flooded treatment for *Z. nicaraguensis*, the degree of aerenchyma formation increased at three weeks after sowing, and was greater in four-week old plants, in particular in roots emerging at the second nodes. Overall, the degree of aerenchyma formation in *Z. nicaraguensis* in non-flooded

treatments is less than in flooded treatments (Figure 3).

Experiment 2: Screening accessions for aerenchyma formation without flooding

Lines or species exhibiting high levels of aerenchyma formation in non-flooded conditions may be useful in providing flooding tolerance to

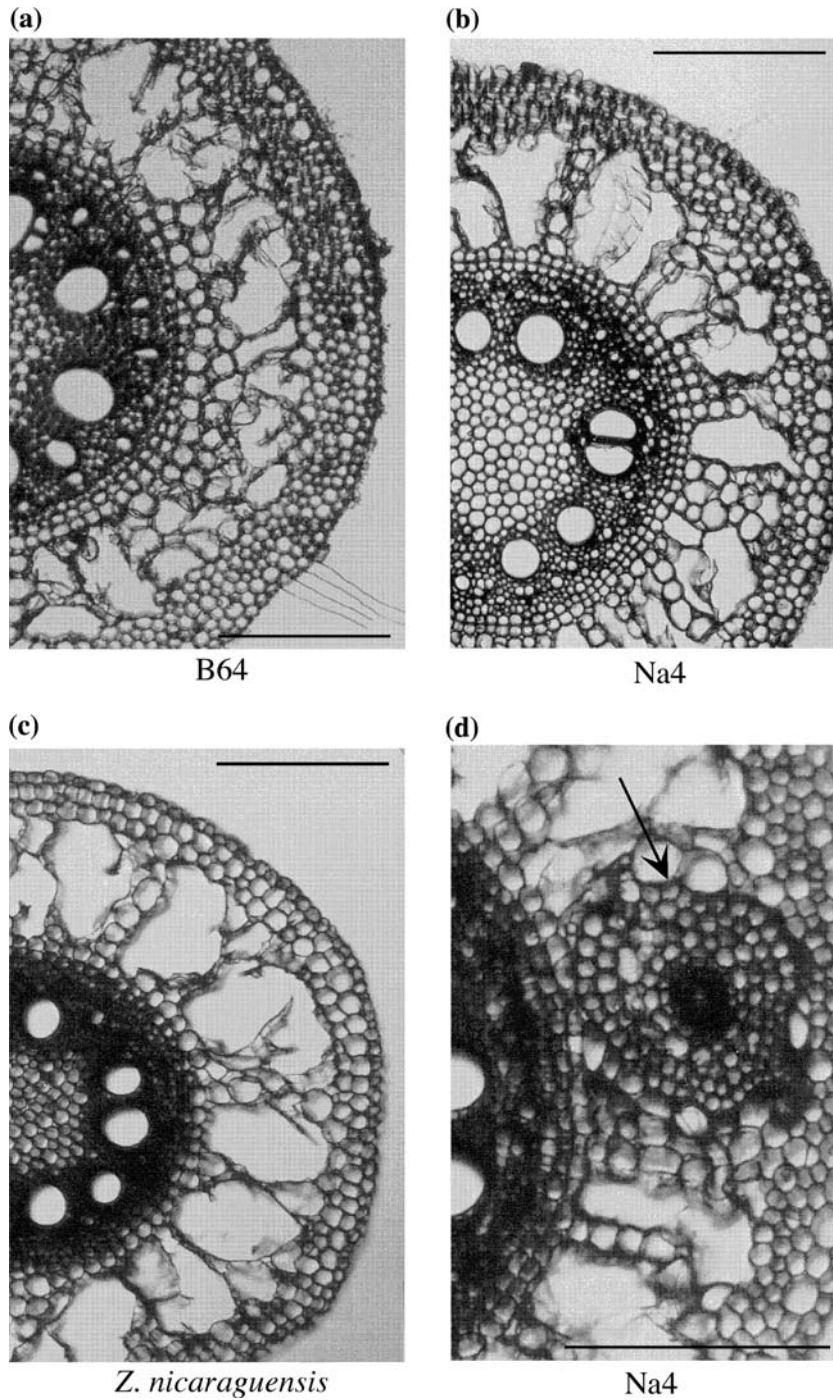


Figure 2. Cross sections of adventitious roots that emerged from the second node when flooded for two weeks (0.5 cm from the root-shoot junction) showing aerenchyma in (a) B64 (score 2), (b) Na4 (score 2) and (c) *Z. nicaraguensis* (score 3). (d) Small root in aerenchyma channel in Na4 (arrow). No aerenchyma was present in similar sections from non-flooded B64 and Na4. Bar = 0.25 mm.

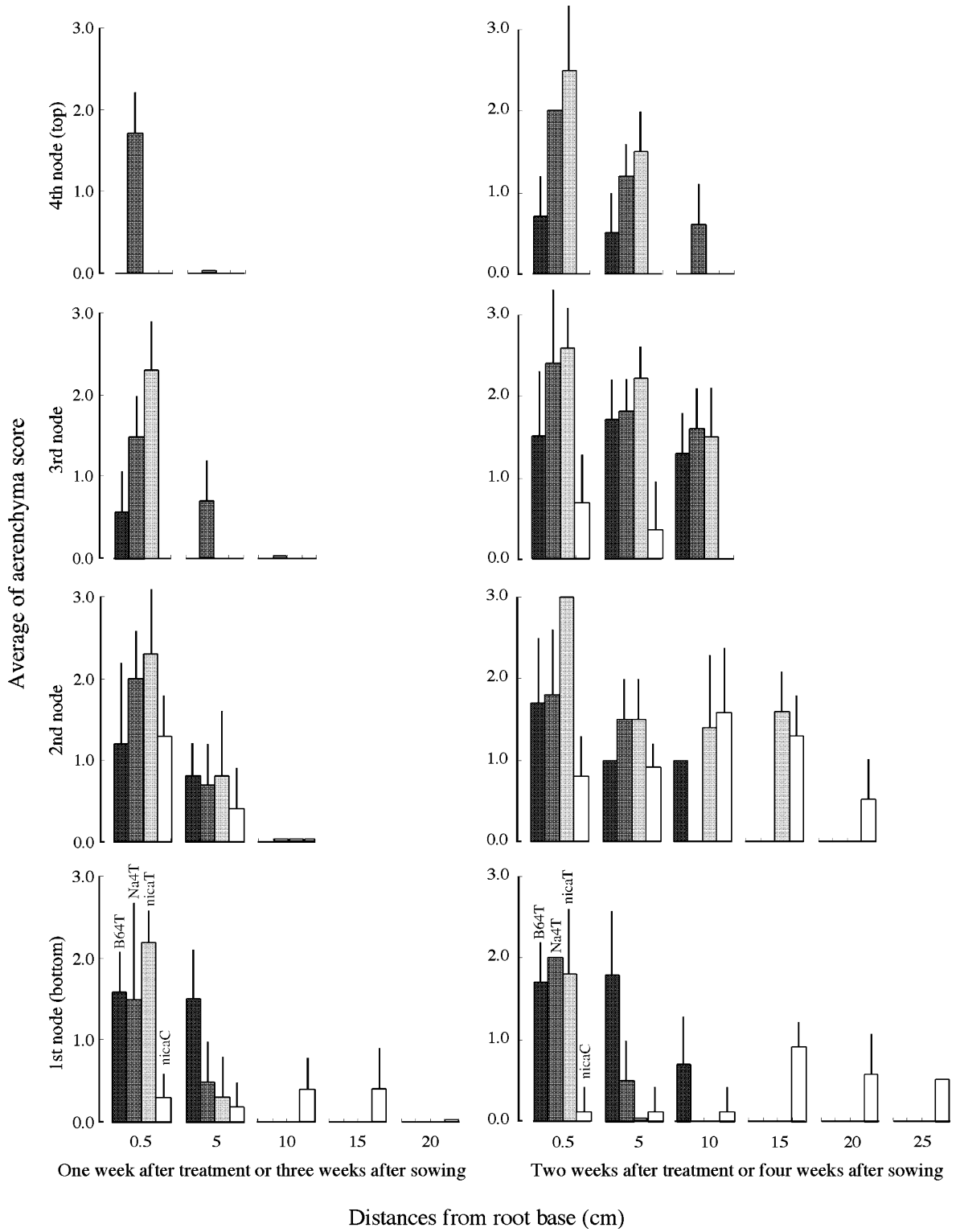


Figure 3. Comparisons of aerenchyma-forming capacity among three accessions with flooding treatment (shaded bars) and non-stressed control (white bars, only shown for *Z. nicaraguensis*) with one week of treatment or three weeks after sowing (left) and with two weeks of treatment or four weeks after sowing (right). The values are the means of 4–6 roots \pm standard deviations. Absence of the standard deviation bar indicates zero variation about that mean value. Average lengths of roots evaluated for aerenchyma formation were presented in Figure 1.

maize. Based on the results of Experiment 1, we evaluated adventitious roots that emerged from the second nodes of four-week old plants in drained soil. Of the 17 maize accessions evaluated without flooding, B55 and Mo20W were observed to form aerenchyma, and N196, A15 and CML-155 exhibited a low but still visible degree of aerenchyma formation (Table 1). Examples of aerenchyma formation in these maize inbred lines are presented in Figure 4. The remaining 12 accessions did not form aerenchyma in any portion of the adventitious roots at second nodes. In addition, when the degree of aerenchyma formation was evaluated in the first- and/or third-node adventitious roots of these 12 accessions, no aerenchyma was observed (data not shown).

Of the four teosintes evaluated in this non-flooding experiment, *Z. nicaraguensis* and *Z. luxurians* formed aerenchyma, whereas *Z. mays* ssp. *huehuetenangensis* and *Z. mays* ssp. *mexicana* did not (Table 1). The degree of aerenchyma formation in roots obtained from the second node of non-flooded plants are presented in Figure 5. Aerenchyma formation is observed to be higher in *Z. nicaraguensis* and *Z. luxurians* than in the five aerenchyma-forming maize lines.

Discussion

Using teosinte and maize materials showing varied levels of flooding tolerance at the seedling stage, we have found that *Z. nicaraguensis* exhibits the capacity for aerenchyma formation during both flooded and non-flooded treatments. In addition, *Z. luxurians*, which is known to develop aerenchyma at the adult plant stage (Ray et al., 1999), was also observed to form aerenchyma during non-flooding treatments at the seedling stage. We have further found that maize inbred lines, B55 and Mo20W, form significant aerenchyma in non-flooding conditions. These materi-

als may be useful genetic resources for the development of flooding-tolerant maize accessions.

Overall, the higher degree for the capacity to form aerenchyma was observed in teosinte (Figure 5). This was not surprising since wild species have often provided good genetic resources for the introduction of superior levels of biotic or abiotic stress tolerance (Harlan, 1976). In wild *Hordeum*, for example, there is a greater tendency for aerenchyma formation than that observed in cultivated barley when the treatment consisted of a stagnant deoxygenated nutrient solution (Garthwaite et al., 2003; McDonald et al., 2001). All four teosintes also indicated a predisposition toward adventitious root formation at the soil surface during flooding (Bird, 2000; Mano et al., 2005a,b). Furthermore, in a greenhouse experiment, *Z. nicaraguensis* showed a high adaptability to soil flooding and low Eh (soil redox potential) conditions that are frequently observed in the flooded upland paddies and typically cause severe damage to plants (Y. Mano, unpublished). Given these three traits, teosintes may provide a superior genetic resource for the development of flooding-tolerant maize accessions.

Two types of aerenchyma have been reported: lysigenous aerenchyma and schizogenous aerenchyma (Evans, 2003). Based on the morphology of the aerenchyma observed in this study, it can be considered lysigenous. During an earlier study regarding the molecular and cellular analyses of lysigenous aerenchyma formation, Drew et al. (2000) summarized the pathway of aerenchyma formation as being hypoxia \rightarrow ACC (1-aminocyclopropane-1-carboxylic acid) synthase \rightarrow ACC oxidase \rightarrow ethylene \rightarrow selective cortical cell death \rightarrow aerenchyma formation. In the development of lysigenous aerenchyma, additional factor(s) other than hypoxia that affect ACC synthase and/or ACC oxidase induction, may be inducing aerenchyma formation in *Z. nicaraguensis* and *Z. luxurians* at drained condition (this study) and in other aerenchyma-forming species

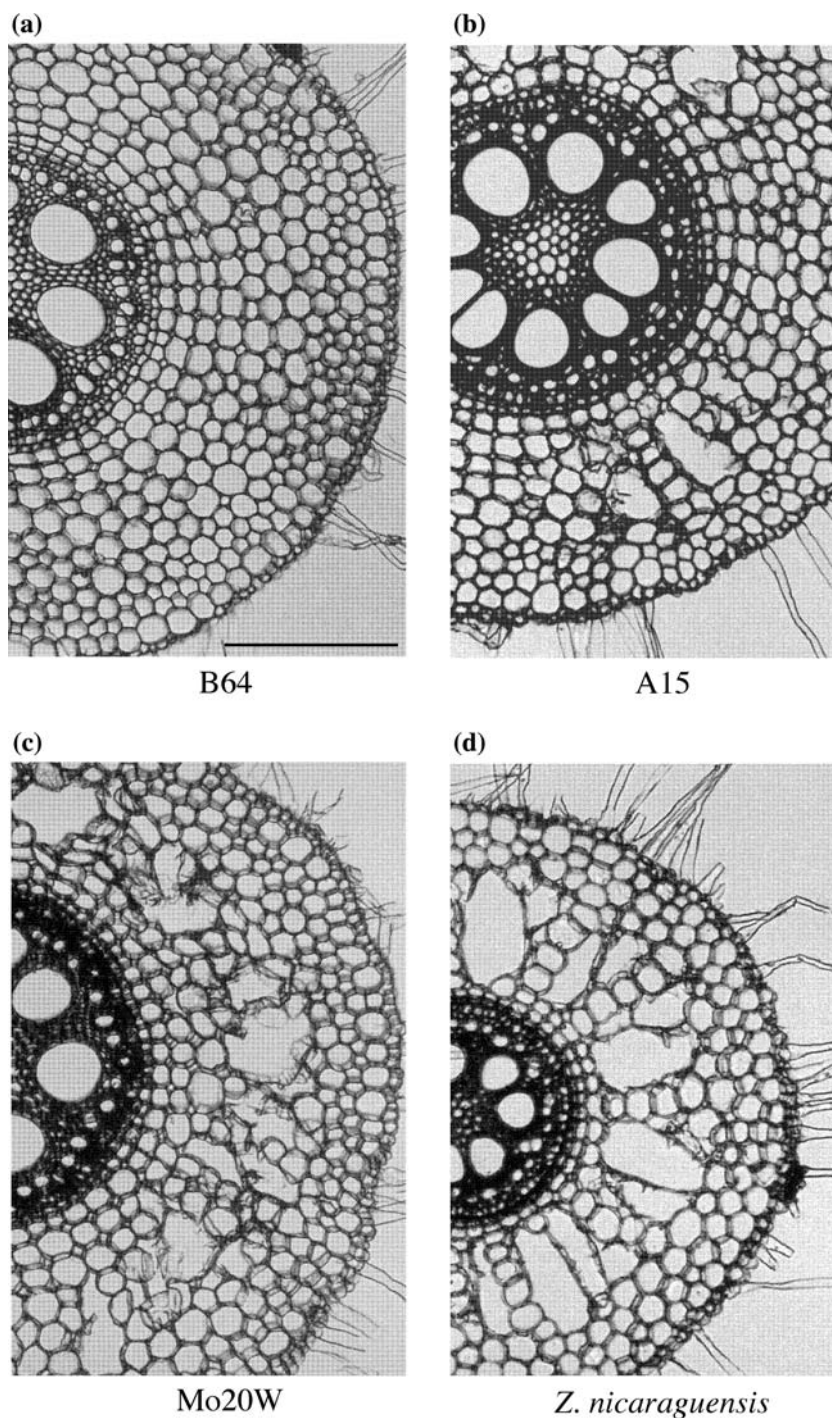


Figure 4. Cross sections of adventitious roots that emerged from the second node in four-week old seedlings when not flooded (15–20 cm from the root base) showing the lack of aerenchyma of (a) B64 (score 0) and showing aerenchyma in (b) A15 (score 0.5), (c) B55 (score 1), and (d) *Z. nicaraguensis* (score 2). Bar = 0.25 mm for all.

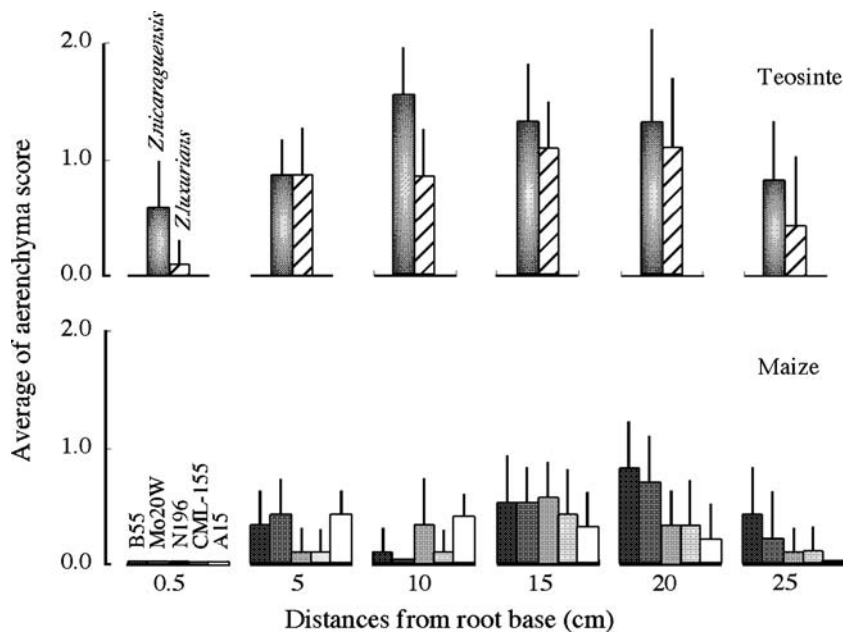


Figure 5. Capacity to form aerenchyma in adventitious roots at the second node when in drained soil (i.e. not flooded), in two aerenchyma-forming teosinte species (top) and five maize accessions (bottom). The values are the mean of 8 roots \pm standard deviations. Average lengths of roots evaluated for aerenchyma formation were 30 ± 3 cm (average \pm standard deviation) for *Z. nicaraguensis*, 30 ± 2 cm for *Z. luxurians*, 31 ± 3 cm for B55, 30 ± 2 cm for Mo20W, 29 ± 1 cm for N196, 30 ± 1 cm for CML-155 and 29 ± 2 cm for A15.

such as rice (Colmer, 2003) and wild *Hordeum* (Garthwaite et al., 2003) in well-aerated solution. Additional research using maize near-isogenic lines with and without teosinte's aerenchyma-forming gene that are in development may clarify this situation.

In an earlier study (Mano et al., 2002), flooding tolerance at the seedling stage was evaluated for 17 maize accessions. Their indicated levels of tolerance (T; tolerant, M; moderate, S; sensitive) are provided in Table 1. The non-aerenchyma-forming in drained conditions but flooding tolerant line Na4 exhibited an extremely high capacity for adventitious root formation at the soil surface during flooding (Mano et al., 2005a,c) and this characteristic may result in its higher capacity to avoid the stress associated with flooding. The remaining two non-aerenchyma-forming in drained conditions but flooding tolerant maize accessions, B73 and Na74, exhibited a moderate to low capacity for adventitious root formation and may have other factors such as anaerobic catabolism (e.g. ADH1 and ADH2; Subbaiah and Sachs, 2003) that allow them to be tolerant of flooding conditions.

During flooding conditions, small lateral roots were observed to form within some aerenchyma channels (Figure 2d). This unique morphology was unanticipated; however, the presence of small lateral roots in aerenchyma channels has been reported in eastern gamagrass (*Tripsacum dactyloides*) when grown in claypan soils (Clark et al., 1998). Claypan soils have a high capacity to hold water, and the potential for flooding and anaerobic conditions is high. Also in rice, sulfide-induced lateral root growing through the adventitious root cortex (aerenchyma) has recently been reported (Armstrong and Armstrong, 2005). It is unclear at this time if the anatomy and function of these small internal roots are related to those observed in *Tripsacum dactyloides* and rice.

In conclusion, we have identified materials exhibiting a high capacity to form aerenchyma that may serve as a useful genetic resource for genes controlling aerenchyma formation. QTL associated with this trait are being identified using segregants in B64 x *Z. nicaraguensis* and B73 x *Z. luxurians* populations. By combining QTLs associated with aerenchyma formation and

adventitious root formation at the soil surface (Mano et al., 2005b,c), it may be possible to develop maize that tolerates soil flooding by avoiding hypoxia/anoxia in the roots.

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